

BIONOMICS OF TWO ASPEN BARK BEETLES,
TRYPOPHLOEUS POPULI AND *PROCORYPHALUS MUCRONATUS*
(COLEOPTERA: SCOLYTIDAE)

Jerold L. Petty¹

ABSTRACT.—Beetles of *Trypophloeus populi* attacked green bark of unhealthy aspen (*Populus tremuloides*) and hastened the death of the tree. Beetles of *Procryphalus mucronatus* favored dead bark and were of little significance in the death of the aspen. These two beetle species were distinguished from each other by their primary galleries, eggs, larvae, larval mines, and mating behavior. In *T. populi*, there were three larval instars and one to one and one-half generations per year; only larvae overwintered, and the eggs of the first generation were present by mid-July. In *P. mucronatus*, there were two larval instars and one and one-half to two generations per year; both larvae and adults overwintered, and the first eggs of the new season were present by late May.

In North America, quaking aspen (*Populus tremuloides* Michaux) occurs coast to coast from the 49th to the 69th parallel and sporadically at the higher elevations in the southwestern United States and in Mexico (Little 1971). These trees average from 12 to 15 m in height and from 30 to 60 cm in diameter (Preston 1969).

Aspen are important in several ways. Their role is well known as an intermediate (subclimax) cover species in plant succession, leading to the climax coniferous community (Oosting 1956, Krebill 1972). They recover quickly after extreme disturbances such as fire and clearcutting (Preston 1969). Directly, they provide browse for deer, elk, and livestock (Reynolds 1969, Wallmo 1972). Indirectly, they provide for a rich understory that in turn provides habitat for a diverse fauna and forage for livestock (Harper and Warner 1972). In the Rocky Mountains, the poplars (especially aspen) are the most important broadleaf trees and the only ones that could be considered usable as timber (Davidson and Hinds 1968). Aspen can produce more wood over a shorter period of time than conifers at comparable elevations (Davidson, Hinds, and Hawksworth 1959). Recently, they have become important as a timber resource (Lamb 1967). Aesthetically, anyone who appreciates nature cannot deny the unequalled

beauty of a mountainside of aspen, especially in their cadmium hues of autumn.

The only American Scolytidae known to infest the bark of quaking aspen are *Procryphalus mucronatus* (LeConte), *Trypophloeus populi* Hopkins, and *T. thatcheri* Wood. Another scolytid, *Trypodendron retusum* (LeConte), attacks aspen, but it is a wood-boring ambrosia beetle. The published research on *P. mucronatus*, *T. populi*, and *T. thatcheri* has been mainly taxonomic. In fact, virtually nothing of a nontaxonomic nature has been written on the genera *Procryphalus* and *Trypophloeus*. Exceptions are a one-page article on the habits of the European *Trypophloeus binodulus* (Hagedorn 1904) and a half-page article on four European and Asian *Trypophloeus* spp. (Palm 1959).

There are only four known species of *Procryphalus* in the world, two in northern North America and two in northeastern Asia. In North America, *P. utahensis* Hopkins breeds in *Salix scouleriana* (Scouler Willow) and *P. mucronatus* in *Populus tremuloides*. There are 15 recorded localities for *P. mucronatus*, all of which are in the United States: Colorado 7, Idaho 2, New Mexico 2, and Utah 4 (Wood in press).

About a dozen species of *Trypophloeus* occur in Europe and Asia, but only four in North America. Of these four, *T. populi* and

¹Department of Zoology, Brigham Young University, Provo, Utah. Current address: 576 Eastland North, Twin Falls, Idaho 83301.

T. thatcheri are the only ones that have been collected from *P. tremuloides*. *Trypophloeus populi* also breeds in *P. acuminata* (Lanceleaf Cottonwood), *P. angustifolia* (Narrowleaf Cottonwood), and *P. trichocarpa* (Black Cottonwood). There are 13 recorded localities for *T. populi*: Arizona 1, Colorado 1, Nevada (eastern) 1, Utah 6, Idaho 1, Manitoba 1, New Brunswick 1, and Saskatchewan 1 (Wood in press).

The objectives of this paper were: (1) to report investigations on the life history and habits of *T. populi* and *P. mucronatus*, and (2) to determine the nature of the damage they cause in the host. Emphasis was placed on the differences between the two beetles in habits and behavior. It is hoped this research will establish a better understanding of the ecological significance of these species and provide a foundation for further studies of these and related scolytid species.

MATERIALS AND METHODS

Four sites were selected for this study, all of which were in Utah County, Utah. More than 80 percent of the total number of trees on each site were *Populus tremuloides*. The sites covered approximately 3,000 m² each and ranged from 2,256 to 2,377 m in elevation. The sites were initially selected by locating scolytid-infested aspen. The periods of study for each site and further details on the elevation, number of trees studied, and exact location of sites are given in Table 1.

Throughout the study, periodic collections and observations were made at the field research sites and in the laboratory at Brigham Young University from material

brought from the sites. To facilitate observations, scolytid galleries were exposed by cutting away the bark with a razor-blade scalpel.

To rear the beetles, infested bolts, limbs, and bark sections were placed in 20-gallon, galvanized steel garbage cans, each of which had a pint glass bottle attached to collect the emerging scolytids. All rearing was conducted in the laboratory at room temperature. The number of larval instars was determined by measuring the width of the head capsules (Lekander 1968). Head capsules were measured from undamaged larvae and with an ocular micrometer scale in a microscope at 80X magnification. The drawings of the larval head capsules (Figs. 22, 23) were composed from viewing 25 specimens of each beetle species under the light microscope and from 18 scanning electron micrographs of four specimens of each species. Photographs were taken with a Yashica 35 mm SLR camera equipped with extension tubes and a flash. The margin of a millimeter ruler was included in many of the photographs for measurements. Details of the territorial behavior and mating ritual were obtained from extensive observations in the field and from movies obtained in the field with a Vivitar 8 mm movie camera equipped with a close-up lens.

A fungus was cultured from adult bark beetles by macerating them on the top of sterile pieces of aspen wood (four beetles per piece), and then placing each piece of wood upright on agar-agar medium inside petri dishes. The petri dishes were maintained at room temperature in the labora-

TABLE 1. Descriptions of research sites, Utah County, Utah.

Site No.	Locality	Elevation (m)	Pm*	Tp*	B*	DBH (cm)	Study period
I	1.6 km N Aspen Grove	2,256-2,259	8	2	2	30-50	VII-1972 to VI-1976
II	1.7 km N Aspen Grove	2,274-2,286	14	18	8	10-48	VII-1972 to VI-1976
III	2.4 km N Aspen Grove	2,365-2,377	0	12	2	31-49	VII-1975 to VI-1976
IV	1.9 km NE Squaw Peak	2,323-2,332	8	0	0	30-40	V-1973 to XI-1974

*These columns indicate the number of aspen trees studied at each research site that were infested with only *Procrpyhalus mucronatus* (Pm), with only *Trypophloeus populi* (Tp), and with both beetle species (B).

tory. When the fungus had grown out into the agar, the agar was removed intact and placed on the bark of a living aspen tree. To inoculate the tree, a razor-blade scalpel was inserted repeatedly into the bark by passing it through the agar. The agar was left on the tree. Three agar plates were used per tree. Subsequent observations were taken to determine whether or not the trees were dying. Three trees were inoculated in June and observed twice a month until October. The following year three observations were taken from June to October.

RESULTS AND DISCUSSION

Trypophloeus populi

BEHAVIORAL SEQUENCE.—After locating the host tree, the female landed on the bark of the aspen and searched for a suitable site to begin the entrance of her primary gallery. When one female encountered another female who had already started her gallery, she paused and then continued her search, or tried to remove the other female and take over her entrance (see Territorial Behavior).

The site selected by the female to start the gallery was usually at a slight rough spot or irregularity on the surface of smooth living bark (Table 2). This apparently gave her better leverage to start the entrance. Sometimes this site was on or at the edge of a rough black spot (Fig. 4). The black spot made it difficult to see the beetle. This site was on the bole, limbs, or branches as small as 10 mm diameter.

Typically, the female directed the entrance into the bark at about a 30-degree angle from the surface (Figs. 14, 28) and upward from the horizontal (Table 2 and Fig. 3). In completed galleries, the entrance tunnel was about 2.5 mm in length and entered the primary egg chamber from the side (Table 2 and Fig. 1).

While the females were initiating their galleries, males (that had located the tree) began to search for them. When a male located a female that was initiating the gallery, he either stopped briefly and then went on to find another female, or he cop-

ulated with her (Figs. 14, 15) and then moved on.

The male behaved in a different way when the female was below the surface of the bark. After she backed up to the surface of the bark to remove boring dust, he mounted her (Fig. 28). Then, he tried to position himself and the female for copulation. He did this by vigorously stroking her with all of his legs. It appeared as though he was running in place. If successful, copulation followed, but usually this was repeated several times before copulation took place.

The female repeatedly backed part way out of and then returned into the gallery. Either this was part of her mating behavior



Fig. 1. *Trypophloeus populi*, primary galleries: 10 of the 13 galleries pictured were exposed by cutting away the epidermal bark covering them: e, white pointer marks the gallery entrance; black pointer, the parental adult exit hole; ft, the food tunnel; the circled arrow points upward.

TABLE 2. Details of 40 primary galleries from 4 trees (10 galleries each) 9 March 1976 (*Trypophloeus populi*).

Listing	Category	No. of Galleries
Bark surface at entrance	Slightly rough or irregular (Fig. 20)	31
	Black rough spot, entrance at edge (Fig. 4)	5
	Black rough spot	4
	Smooth	0
		Total 40
Blockage of entrance	Partially filled w/frass	18
	No blockage	18
	Plugged w/dead male	4
		Total 40
Angle of entrance above or below horizontal (degrees)	1-45 above	23
	46-90 above	9
	0-45 below	9
	46-90 below	0
		Total 41 ^a
Bark covering gallery	Medium split (Fig. 6)	20
	Slight split (Fig. 1, unexposed galleries)	16
	Extreme split (Fig. 20)	4
		Total 40
Parents (dead) in the 14 galleries w/secondary chambers. ^b	Male and female ^c	7
	Female only ^d	4
	Male only	0
	Neither parent	3
		Total 14
Parents (dead) in the 26 galleries without secondary chambers. ^e	Unoccupied	17
	Male and female	5
	Male only	2
	Female only	2
		Total 26

^aOne gallery had two entrance holes.

^bExit holes were not present in any of the secondary chambers, and the epidermal bark covering them was not split.

^cIn all seven galleries, the female was blocking the food tunnel entrance to the secondary chamber.

^dIn all four galleries, the female was blocking the food tunnel entrance to the secondary chamber.

^eThere were 26 exit holes: 18 in the food tunnel and 12 in the primary chamber.

or she was continuing her excavations. This interrupted the male's attempts to copulate with her. Because of the angle of the entrance into the bark, it was necessary for the female to back out of the entrance at least one-fourth of the way to be available for copulation.

After copulation, the male entered the gallery behind the female. If the gallery was not deep enough to accommodate both, the male entered as far as possible while the female continued to lengthen the tunnel.

As long as the male was protruding above the surface of the bark, another male could challenge him for his claim. This territorial competition was similar to that between females (see Territorial Behavior).

The female devoted her time to the excavation of the gallery, to oviposition, and probably to repeated copulation inside the gallery (observed on two occasions). She excavated the cavellike primary egg chamber at the inner end of the entrance tunnel. The design of this chamber was varied (Figs. 1, 2, 3) and sometimes consisted of two or even three distinct areas for the deposition of eggs. The female deposited a cluster of approximately 14 eggs in the primary egg chamber. They were deposited near to or against the paper-thin epidermal bark covering the gallery. Here, heat from the sun may have facilitated incubation, and aeration through the bark surface may have inhibited or prevented bacterial or fungal growth. Sometimes two or three clusters of eggs were laid in one gallery. Additional clusters contained fewer eggs (see Eggs). Very often a lone egg or two were deposited elsewhere in the gallery (Fig. 3). If eggs were located below subsequent excavations, frass accumulated on them (Fig. 2).

From the primary chamber, the female usually excavated a food tunnel (Figs. 1, 5, 6, f.t.) that was usually directed upward and extended approximately 10 mm. Frass collected in the tunnel behind her. Sometimes, she excavated a side pocket and deposited a few eggs therein. At the end of the food tunnel, she either died, exited by boring out of the tree, or excavated a secondary egg chamber (Figs. 5, 6, s.c.).

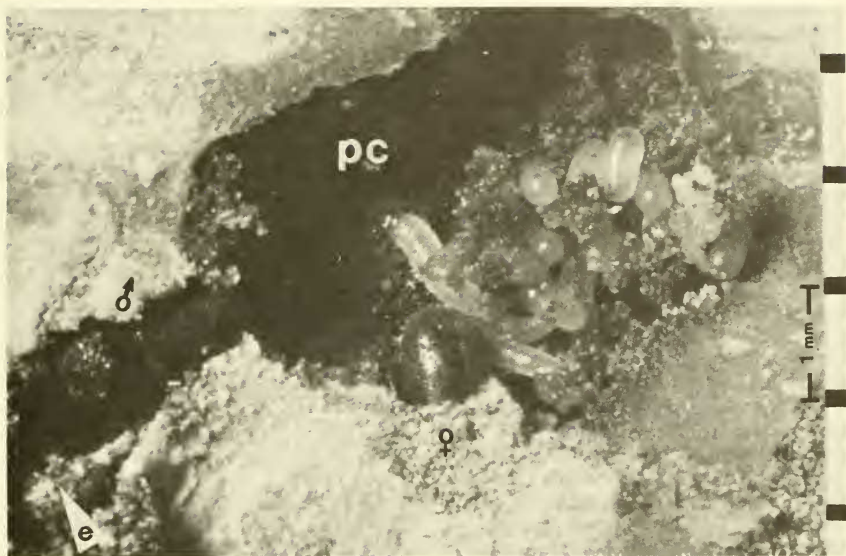


Fig. 2. *Trypophloeus populi*, partially exposed new primary gallery: pc, primary chamber.

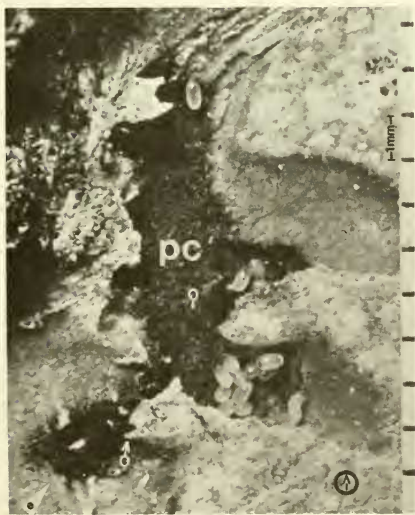


Fig. 3. *Trypophloeus populi*, exposed new primary gallery: pc, primary chamber; circled arrow points upward; parents (male blocking entrance), one and one-half egg clusters, and one lone egg.

During the period of excavation and oviposition, the male blocked the entrance to the gallery with his body (Figs. 2, 3). He died in this position, abandoned the gallery (by way of the entrance or by boring out through the bark covering the primary chamber), or followed behind the female as she excavated the food tunnel. Either one or both died or exited at or near the end of the food tunnel (Table 2). When the female excavated a secondary egg chamber, the male (if present) usually blocked the food tunnel at the point where it entered the secondary egg chamber (Fig. 5, s.e.) and helped remove boring dust by packing it behind himself in the food tunnel.

Once an egg hatched, the larva began its larval mine by boring into the wall of the primary gallery. As the mine in previously unexcavated bark was lengthened, it was also widened according to the growth of the larva. The dark brown to black frass deposited by the larva accumulated behind it and filled the mine. Here, it stuck together and dried, forming a firm blockage. The

walls of the frass-filled mines were stained a dark brown color (Fig. 7). The larva excavated the first portion of its mine just under the bark epidermis (Figs. 6, 7). The length of this part of the gallery was approximately 20 mm, but this varied depending on the condition of the host, time of year, density of galleries, etc. This portion followed either a straight course, meandered, or reversed direction abruptly (Figs. 6, 7). At the end of this shallow excavation, the larva mined deeper into the bark (Fig. 6).

When the larva was mature, it excavated a frass-free pupal cell. In this cell it pupated and transformed into an adult. The new adult bored out of the bark and flew to find another tree to repeat the life cycle.

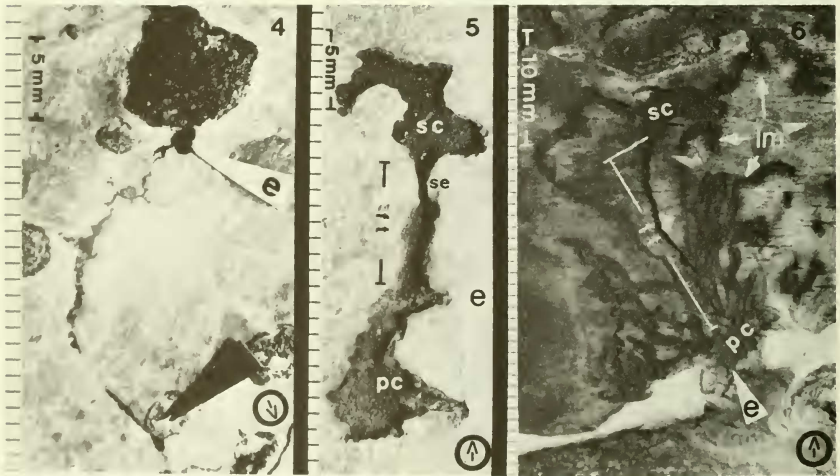
PRIMARY GALLERY.—Forty primary galleries, which had been excavated by bark beetles (*T. populi*) the previous season, were studied 9 March 1976 (Tables 2 and 3). Fourteen of the 40 had a secondary chamber. The bark lining the secondary chambers was darker in color (apparently stained) than in the primary chambers (Figs. 5, 6). In all 14, the bark covering the primary egg chamber and food tunnel leading

to the secondary chamber was split, but this split did not extend into the secondary egg chamber.

Normally, each gallery was shared by one parental male and female. Occasionally one

TABLE 3. Measurements and details of 40 primary galleries from 4 trees (10 galleries each) 9 March 1976 (*Trypophloeus populi*).

Category	$\bar{x} \pm \text{SD}$	Range	n
Entire length	21 ± 7.2	(10-14)mm	40
Maximum depth	$2 \pm .86$	(1-5)mm	40
Maximum width	4.6 ± 1.2	(3-8)mm	40
Length of primary egg chamber	10.6 ± 2.8	(7-20)mm	40
Length of food tunnel	10 ± 4.2	(3-20)mm	20
Gallery orientation expressed in degrees to the vertical	72 ± 25.9	(0-90) $^\circ$	40
Percent of gallery filled with frass	60.5 ± 25.9	(10-90)%	40
Percent of food tunnel filled with frass	67 ± 30.7	(0.90)%	20



Figs. 4-6. *Trypophloeus populi*, details of three primary galleries (e, white pointer), parental adult exit hole (black pointer), primary chamber (pc), secondary chamber (sc), secondary entrance (se), food tunnel (ft), the circled arrow points upward; 4, split bark covering primary gallery; 5, bark covering primary gallery removed; 6, bark covering primary gallery and larval mines removed.

gallery was connected to a neighboring one. Some galleries contained from one to three entrances. Excess parental adults appeared to be permanent residents of the gallery. The frequency of these exceptions was highly variable and increased with increased density of the beetles. Of the 10 exposed galleries in Fig. 7, one had two entrances, one contained a lone female, and one contained three females.

The angle of the entrance into the bark enabled the male to effectively block the entrance. In his blocking position the posterior surface of his elytra completely covered the entrance opening (Fig. 3, e). If the entrance had been more nearly perpendicular to the bark surface, as in *P. mucronatus*, the ventral side of the posterior end of his abdomen would have been visible from the bark surface, and his elytra would not have completely covered the opening. This would have been to the advantage of predators, and rain could have entered the gallery more easily. The angle of the entrance into the bark, and the fact that it was usu-

ally directed upward from the horizontal, facilitated removal of frass and boring dust. In *P. mucronatus*, the entrance was often plugged with frass instead of the male.

The food tunnels studied were approximately 10 mm long. The reasons for the relatively great length of the food tunnel were not clearly understood. The fact that this tunnel was practically full of boring dust indicated that much more bark was excavated than was ingested by the female parent. Much of the boring dust found in the old primary galleries may have come from the excavation of the first part of this tunnel. The food tunnel may hasten the death of the bark in the surrounding area to the advantage of the larvae. The rate of mortality of the immatures was high in bark that remained alive. The greater the distance between a secondary egg chamber and the primary chamber, the less chance there will be of competition for space among the larvae of the gallery.

The fact that in some instances the female excavated a secondary egg chamber



Fig. 7. *Trypophloeus populi*, exposed larval mines: lm, larval mines; l, larva; db, expansion of dying bark; pa, parental adult; E, edge of epidermal bark not cut away; G, primary gallery; white pointer (e), entrance to primary gallery; black pointer, parental adult exit hole; the circled arrow points upward.

and oviposited therein and in other instances she exited, indicated that if she did exit she was capable of excavating another primary gallery and ovipositing there also. Whether or not the female exits at the end of the food tunnel may be a function of the condition of the bark or the proximity of other galleries. If gallery density is high, it is expected that the incidence of secondary chambers would be low.

The male's habit of following the female while in the food tunnel suggests that he may copulate again with the female. His position at the food tunnel entrance may also prevent predators from entering.

EGGS.—The eggs were oblong, white, translucent, and had a tacky surface (Figs. 2, 3). Of 52 eggs measured, the mean width and length were $.33 \pm .030 \times .65 \pm .097$ mm (Range $.27-.42 \times .55-.77$ mm).

To estimate the number of eggs laid per gallery, the eggs and larvae in five primary galleries found 14 July 1973 were counted. The quantities per gallery were: 18 eggs and 3 larvae, 6 and 4, 11 and 6, 22 and 2, and 11 and 4. The parental adults were present and oviposition was probably not completed.

A primary gallery initiated 13 July 1974 and examined 3 August 1974 (21 days later) contained 15 eggs and 4 larvae (11 eggs and 3 larvae in one cluster, and 4 eggs and one larva in another). The gallery was 1.5-3.5 x 13 mm. Both parents were present and alive, the male blocking the entrance.

The tacky surface of the eggs normally held them together in a cluster in one area of the gallery. When frass fell on them, it adhered loosely. Apparently the parents did not remove this debris from the eggs because the eggs might be removed also.

Apparently the primary gallery protected the brood from predators and desiccation long enough for the eggs to hatch and for the larvae to mine out of it. After this, the bark covering the gallery usually split open (Fig. 4). The drying and shrinking of the gallery that followed appeared to make the entrances of the larval mines less accessible to entry by predators.

Predators may gain entry into the primary gallery when the male leaves the en-

trance to feed or copulate inside the gallery, and when the bark covering the gallery splits. The male may not need to leave the entrance to feed. Some of the borings pushed to him by the female might serve this purpose.

There are some problems created by laying the eggs in clusters. Egg mortality factors such as desiccation, predators, bacteria, and fungi would likely destroy whole clusters of eggs at a time compared to one egg at a time if they were oviposited as in *P. mucronatus*.

LARVAE.—The larvae were white, legless, and grublike (Figs. 2, 3). They appeared dark when their intestines were full of the brown bark. The relative length, distribution, and number of head capsule setae (Fig. 22) were characteristic of the species. The pattern of sclerotization on the frontal shield (Fig. 22, f.s.) may have been consistent in the last instar.

Widths of the head capsules of 232 larvae (Table 4) and numbers per size class (Fig. 24) indicate that there are three larval instars. Those $.21-.28$ mm, $.30-.38$ mm, and $.40-.50$ mm were categorized as Instar I, II, and III, respectively. These categorizations resulted in four size classes for Instar I, five for Instar II, and six for Instar III (Fig. 24).

In 24 scolytid species, Lekander (1968) found the average increase in larval head capsule widths from one instar to the next was 1.32 times (limits 1.20 and 1.48 times). By applying his method to *T. populi*, the average head capsule width increase (index) from Instar I to II and II to III was 1.31 and 1.35 times, respectively, compared to 1.33 from Instar I to II in *P. mucronatus*. The width of the head capsule in the last larval instar of *T. populi* was considerably wider ($.46 \pm .022$ mm) than that of *P. mucronatus* ($.36 \pm .021$ mm).

LARVAL MINES.—The larval mines were distinct and clearly separate from the primary gallery and usually from each other. The expansion of the dying bark surrounding the larval mines (Fig. 7, d.b.) indicated that the excavation accelerated the decline of the tree. The dark stain observed lining the mines may have been from oxidation of the bark or frass or both, or it may have

been from fungi or bacteria associated with the beetle.

A dead tree in which emergence had taken place was examined 9 March 1976. The length of 16 larval mines (randomly selected) was from 26 to 42 mm (33 ± 4.5 mm). For additional information, larval depths and distances away from the primary gallery were measured from four trees containing live larvae 9 March 1976 (Table 5).

ADULTS.—Beetles were reared in the laboratory on various dates to determine the sex ratio and body lengths of the male and female (Table 6). The total reared (438 males and 587 females) gave a sex ratio of 1:1.34. A ratio of 1:1 was expected because of the importance of the parental male in blocking the gallery entrance.

From the 100 adults reared 7-13 April 1976 (Table 6), the first 50 to emerge (7-8 April) were longer ($1.86 \pm .106$ mm, males, and $2.0 \pm .097$ mm, females) than the second 50 ($1.8 \pm .124$ mm, males, and $1.9 \pm .130$ mm, females). The same was found in *P. mucronatus*.

In *T. populi*, the males were about 5 percent shorter than the females (widths were not determined). This was not expected because a male that is smaller than a female cannot block the gallery entrance as effectively as one the same size. These measurements were taken from emergent adults. The measurements of paired beetles in the primary gallery at the new tree may reveal less difference because of mortality of the smaller beetle during the flight to the new tree, and/or because of the replacement of

TABLE 4. Width of 232 larval head capsules (*Trypophloeus populi*).

n°	m ± SD	Range (mm)	n**	Index Obtained
131	.26 ± .016	(.21-.28)	7	.46/.26 = 1.71
50	.43 ± .016	(.30-.38)	8	.46/.34 = 1.35
51	.46 ± .022	(.40-.50)	6	.34/.26 = 1.31

*Sample size of larvae.

**Sample size of trees.

the smaller beetle by a larger one in territorial behavior.

OVERWINTERING.—The larvae constituted the overwintering life stage (Tables 7, 8). Instars II and III survived at a higher rate than did Instar I. The contrast in the total number of each instar from one collection date to the next during winter was apparently due to the condition of the bark sampled and the differences in the dates when the trees were attacked.

The differences between the time material was brought into the laboratory for rearing and when the new adults began to emerge (Table 6) and the percentages of feeding larvae on different dates (Table 7), indicated that a dormant period occurred in the overwintering larvae and that it was controlled by something other than daylight and continuous warm temperature, because the rearing was conducted at room temperature and in the dark.

GENERATIONS PER YEAR.—The presence (Table 8), relative abundance of overwintering life stages (Table 7), approximate

TABLE 5. Depth of larvae in bark and proximity to primary gallery 9 March 1976 (*Trypophloeus populi*).

Instar	Distance from primary gallery m ± SD Range (mm)	Depth from sur- face of bark m ± SD Range (mm)	n°	No. of trees sampled and larvae/tree
II	7.5 ± 4.85(1-18)	.75 ± .75(.25-4)	40	2(20)
III	not determined	1.25 ± 1.01(.24-.4)	80	4(20)
III	6.6 ± 2.3(1-22)	not determined	60	3(?)
Total			180	

*Sample size of larvae.

11-month duration of the life cycle in one tree in the field, and approximate 6-month difference between collection date (15 August 1972) and emergence date (February 1973) under laboratory conditions (Table 6), indicated that there were one to one and one-half generations per year in the field.

The overwintered Instar II larvae began to pupate and transform in late June. By early July they were emerging and attacking new trees, and by mid-July they were ovipositing in the new primary galleries (Table 8). This was a late start compared to *P. mucronatus* for the first eggs of the season.

TERRITORIAL BEHAVIOR.—The territorial behavior observed was basically similar to that described for *P. mucronatus*. However, the attempt of one beetle to dislodge the other by extension of the prothoracic legs (Fig. 26) was not observed.

The male that can do the best job of blocking the gallery is apparently selected for both strength and sufficient size to completely plug the entrance. A male that is smaller than the female that excavated the gallery entrance might be more easily displaced than one the same size.

LOCATING INFESTED TREES.—Infestations were found in stands of aspen where there

TABLE 6. Number and length of males and females reared on various dates, 1976 (*Trypophloeus populi*).

Collection date	Emergence dates	♂ (n)	♀ (n)	Lengths ♂ (mm)		Lengths ♀ (mm)	
				$\bar{m} \pm SD$	Range	$\bar{m} \pm SD$	Range
8 Mar ^a	7-8 Apr	18	32	1.9 ± .106(1.7-2.1)		2.0 ± .097(1.7-2.2)	
	9-13 Apr	22	28	1.8 ± .124(1.5-1.9)		1.9 ± .130(1.6-2.1)	
	14-18 Apr	10	13	Not determined		Not determined	
	Totals	50	73				
15 Aug ^b	Feb ^c	59	41	1.9 ± .153(1.5-2.2)		2.0 ± .142(1.7-2.3)	
23 Apr & 24 May ^c	May & Jun	329	471	Not determined		Not determined	
	Grand total	438	587				

^aCollected 15 August 1972 and emerged during February 1973.

^bThe most advanced life stage present was Instar III.

^cThe most advanced life stage present was Instar II.

The most advanced life stage present was Instar II(?). Initial attack of this tree was estimated to be six weeks before collection date.

TABLE 7. Relative abundance of overwintering life stages of *Trypophloeus populi*.

Collection date	No. of trees sampled	Eggs	No. of immatures			Pupae	No. of adults		Feeding larvae (%)***
			Instars				Trans-formed*	Parental**	
			I	II	III				
11 Nov 75	3	51	195 ^a	39	8	0	5 ^c	<10(?)	
9 Mar 76	5	0 ^b	34	194	122	0	0 ^d	0	
23 Apr 76	2	0	3	42	155	0	0	89	
24 May 76	3	0	0	13	67	0	0	(?)	
25 Jun 76	4	0	0	9	139	48	4	(?)	

*In pupal cell or brood tree

**In primary gallery

***Percent of larvae that appeared dark because of bark in their intestines. All the rest were white—their gut devoid of food material.

^aOf these larvae, 55 were dead. Of these 55, 35 were in the primary gallery.

^bThough 6 eggs were collected, they were probably nonviable.

^cOf 54 parental adults collected, 49 were dead.

^dOf 60 parental adults collected, all were dead.

were many trees in the 30 to 50 cm DBH size. Unhealthy or diseased trees, especially those bordering washes, trails, roadways, and seepage areas, appeared to be particularly vulnerable to attack. In summer, the leaves of infested trees were usually stunted and lighter in color than normal. Susceptibility to attack seemed correlated with presence of the artist conk *Fomes appplanatus* (Pers. ex Wallr.) Gill. Trees from which brood had already emerged typically had split bark above the primary galleries and exit holes where the transformed adults had emerged (Fig. 20).

HOST DAMAGE.—The beetles attacked living bark of unhealthy trees (Figs. 8, 9). At site II, 5 of the 18 (27.8 percent) infested trees studied harbored artist conks (*Fomes appplanatus*). Typically, a single tree was attacked en masse, and the tree was covered

with the galleries from the lower bole to the branches. Immature beetles died at a high rate in galleries that were in the smaller branches and in bark that remained alive after attack. The dying bark turned somewhat orange immediately around each gallery (Fig. 7, db.); the orange areas enlarged until they coalesced. The leaves died, the bark turned brown, and, within 3 to 10 weeks after the initial attack, the tree was virtually dead.

Three healthy trees were inoculated June 1973 with a fungus cultured from adult beetles. By July 1974 one of the trees had died; the other two remained healthy.

The decline of infested trees, expansion of dying bark tissue around individual galleries, and the death of one of the three trees inoculated with fungus cultured from adults indicate that this beetle has a definite

TABLE 8. Number of trees by calendar date containing the various life stages of *Trypophloeus populi* and *Procryphalus mucronatus*.

Life stage	Month									
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec-Feb
<i>T. populi</i>										
Eggs	0*	0*	0	0	2	5	2	1	3	0*
Larval Instars										
I	4	1	0	0	4	1	2	1	3	0*
II	4	2	4	3	0	3	0*	0*	6	1
III	4	2	5	5	2	0	0*	1	2	0*
Pupae	0	0	0	5	1	1	0*	0	0	0
Adults in pupal cells	0	0	0	3	1	3	0*	0	0	0
Adults starting primary gallery	0	0	0	0	5	9	0*	0*	0	0
Adults in primary gallery	0	0	0	0	2	3	2	1	4	0
<i>P. mucronatus</i>										
Eggs	0*	0	2	7	7	4	0*	0	0	0
Larval Instars										
I	2	4	2	3	5	1	0*	0*	2	0*
II	2	4	3	0	4	5	0*	0*	4	1
Pupae	0	0	1	0	3	6	0*	0	0	0
Adults in pupal cells	2	2	1	2	8	6	0*	0*	4	1
Adults starting primary gallery	0	2	8	4	3	6	0*	0*	0	0
Adults in primary gallery	1	4	5	6	6	2	0*	0*	0*	0*

*A few eggs were found, but they were probably nonviable.

*This life stage was expected.

role in hastening the decline and death of unthrifty trees. A pathogenic fungus may be associated with the beetle.

The high mortality of immatures in the galleries that were located in bark that remained green after attack indicates that the rapid decline of the tree is essential for survival of the brood.

Unhealthy trees that might otherwise live on for several years evidently die within weeks if attacked en masse by the beetle. This appears to be beneficial to the survival of the aspen stand, since unhealthy trees harbor disease spores and rob understory and new aspen saplings of sunlight and moisture.

Procryphalus mucronatus

BEHAVIORAL SEQUENCE.—The behavioral sequence was basically the same as described for *T. populi*. The observed differences and other details are mentioned here and under subsequent sections.

Adults walking on the bark of the host

held their antennae at right angles to the side of the head. In *T. populi* the antennae were extended forward at an angle of about 45 degrees from the side of the head.

After the male joined the female in the tunnel, the entrance was often blocked with a firm plug of frass. Some of the plugs observed in summer did not completely cover the entrance. Plugged galleries were found that contained only the female parent. Apparently, once the entrance was plugged behind an unpaired female, a male did not join her. Of 37 galleries studied 1 November 1975, the entrances of 35 were plugged completely. Of 90 studied 9 March 1976, all were unplugged. On a few occasions, a dead male was found in the entrance.

Both the male and female excavated the primary gallery. The female excavated the part of the tunnel where the eggs were deposited and the male apparently enlarged the gallery near the entrance (Figs. 16, 17). The female deposited each egg in a niche that she excavated and then packed it in with boring dust. The male apparently fed,



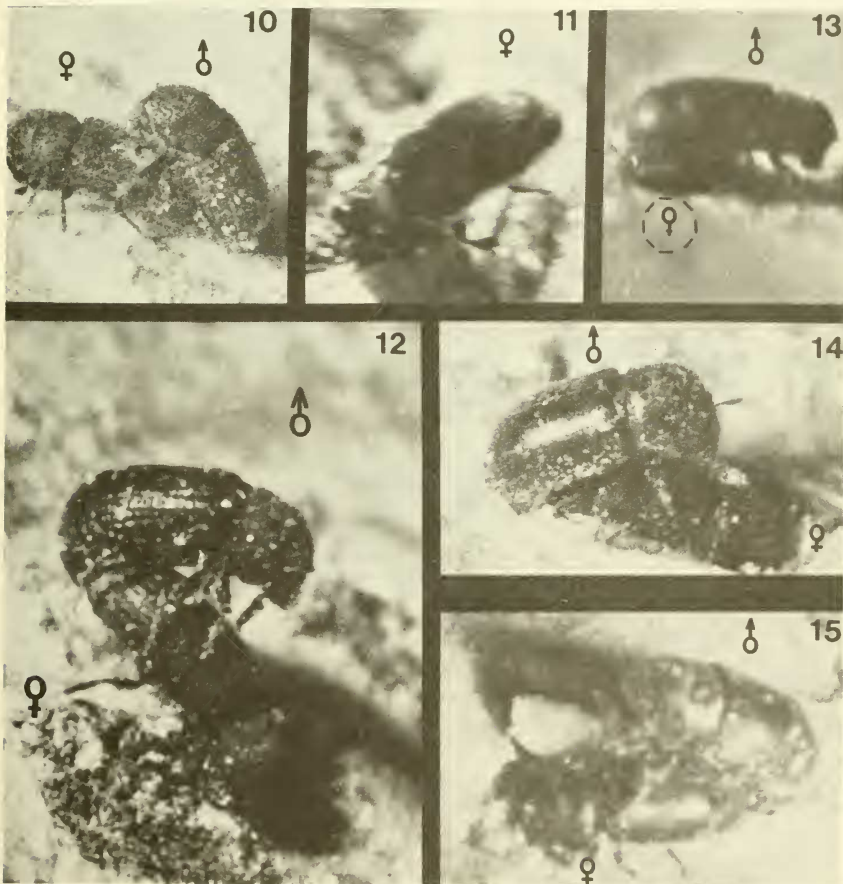
Figs. 8, 9. Aspen tree recently attacked by *Trypophloeus populi*: 8, distribution of gallery entrances (dark spots); 9, leaf condition (green and dying).

and remained available for repeated copulation.

After the eggs were laid, the parents died in the gallery. There was one exception to this. Parent exit holes were found in about 30 percent of the new galleries of two trees 25 June 1976. The trees were quite green. This may have been the reason that some of the parents abandoned the galleries.

After the egg hatched, the larva began to

feed, possibly first on the boring dust that surrounded the egg and then on the walls of the gallery. There appeared to be no relationship between the position of the egg and the direction in which the larva fed. Instar I and II larvae were commonly collected in the primary galleries that they had enlarged (Fig. 18). Instar II larvae and pupae were collected at the end of short larval tunnels (Fig. 19). Unlike *T. populi*,

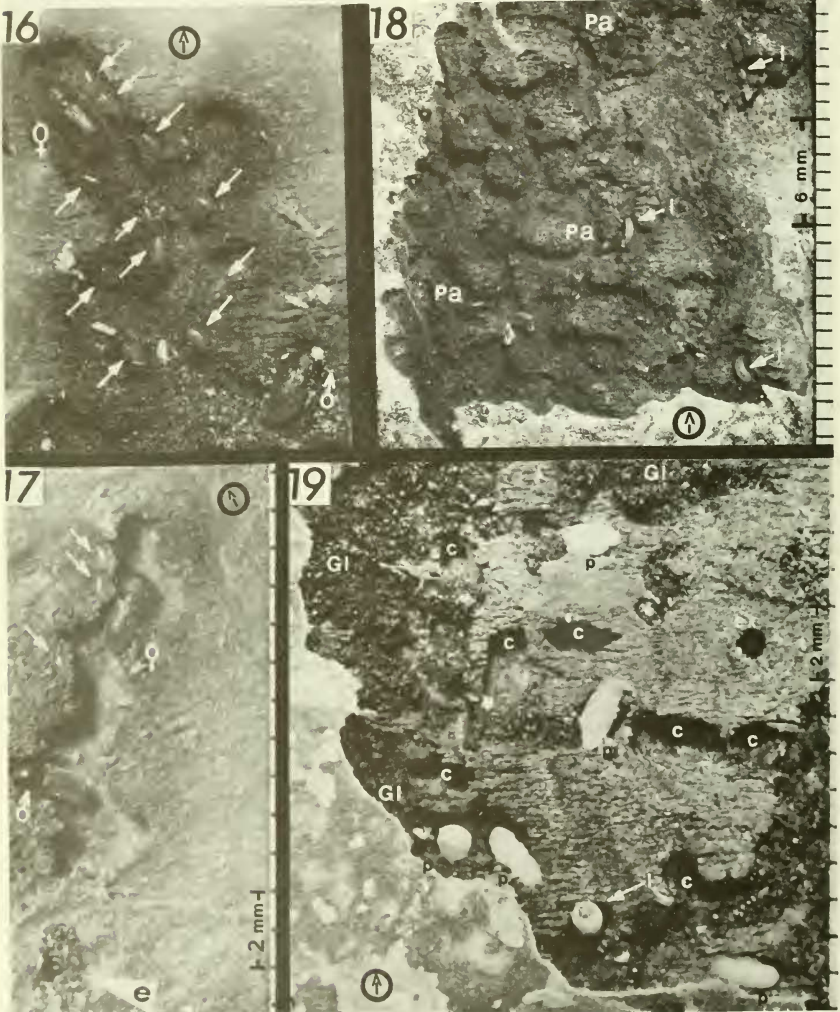


Figs. 10-13. *Procryphalus mucronatus*, mating behavior: 10, male mating with female who is searching for a site to begin the primary gallery; 11, female starting the primary gallery; 12, male copulating with female who is starting the primary gallery; 13, male copulating with female who is in the gallery entrance. Figs. 14, 15. *Trypophloeus populi*, mating behavior: male copulating with female who is starting the primary gallery.

these tunnels were only partially filled with frass and the walls were not stained black.

After the larva was fully grown, it excavated and cleared a cell about .25 mm be-

low the bark surface, where it pupated (Fig. 19) and transformed. After transformation, it fed, emerged, and attacked a new tree to repeat the life



Figs. 16, 17. *Procryphalus mucronatus*, exposed primary galleries: eggs (white arrows), and parents. Figs. 18, 19. *Procryphalus mucronatus*, larval excavations and pupae: pa, parental adult; l, larvae (Instar II); c, pupal cell; p, pupa; ex, exit hole of transformed adult; Gl, primary gallery that has been enlarged by larvae; circled arrow points upward.

cycle. If it was late in the season when the pupa transformed, it overwintered in the pupal cell.

PRIMARY GALLERY.—The primary gallery was: (1) approximately 14 mm long with tunnels from 1 to 3 mm wide that were straight or crooked and branched or unbranched (Figs. 16, 17), (2) usually directed upward (5 to 50 degrees from the horizontal) from the entrance, and (3) kept relatively free from frass. Ten galleries on 23 April 1976 were filled to approximately 35 percent with this debris. Other galleries examined in the summer (Figs. 16, 17) were free of frass. The question arises, how was frass removed when the gallery was plugged? It appeared that bacteria played an important role in reducing the size of the frass particles.

The following information was obtained from 25 galleries located July 1973: All contained eggs and parental adults, but no larvae. Galleries having their central axis approximately horizontal outnumbered two to one those that were approximately vertical (Fig. 17). Four entrances were located at the side, six at the top, and 15 at the bottom of the galleries. Nine of the galleries were fully branched (Fig. 16), 10 slightly branched (Fig. 17), 4 unbranched, and 2 had just been initiated.

Major differences in the primary gallery compared to *T. populi* were: (1) the main gallery was composed of comparatively narrow tunnels instead of broad chambers, and it was usually excavated in dead rather than live bark; (2) the bark of the bole or larger limbs, not the branches, was attacked; (3) the bark was usually soft and fermenting instead of firm; (4) the entrance tunnel was more nearly perpendicular to the bark surface, penetrated deeper into the bark (Fig. 27), and was often plugged with frass instead of being blocked by the male; and (5) the bark above the gallery did not usually split open (Fig. 21) as in *T. populi* (Fig. 20).

The excavation of the primary chamber and food tunnel in *T. populi* resulted in the splitting of the epidermal bark covering them, whereas the excavation of the secondary chamber in *T. populi* and the primary gallery in *P. mucronatus* did not cause the

bark to split. The excavations that resulted in splitting were in dying bark that was green, whereas the excavations that did not result in splitting were in dead bark.

The angle at which the entrance tunnel penetrated the bark (Fig. 27) usually allowed copulation to take place when the male was on the bark surface (Fig. 13) without requiring that the female back out of the entrance. Compared to *T. populi*, the female was more protected in this position, and the male was closer to the bark surface; therefore, presumably both were less conspicuous to predators. The angle of the entrance into the bark may have also facilitated its being plugged because of the slight elbow created where the entrance tunnel curved to become parallel to the surface of the bark. The angle of the entrance, plugging of the entrance of the gallery, and gallery design need further study in relation to the condition of the bark and the time of year when the gallery is excavated.

Eggs.—The eggs were oval, white, translucent, and had a tacky surface (Fig. 16). Of 20 eggs measured, the widths and lengths were .38-.44 mm ($.41 \pm .016$ mm) x .62-.76 mm ($.68 \pm .032$ mm).

Eggs were counted from 20 primary galleries 25 June 1976. Because oviposition was apparently not completed in some of these galleries, only the 10 with the greatest number of eggs were used to compute the mean number of eggs laid per gallery. Galleries with more than one adult female were not counted. The mean was 16.8 eggs (Range 14-20).

Of 20 galleries studied during July 1973, the mean number of eggs per gallery was 8, with limits of 3 and 14; however, oviposition was not complete. Of 23 galleries studied that contained a total of 193 eggs, 95 were on the top, 60 on the bottom, 25 on the right side, and 13 on the left side of the primary gallery. This suggests an order of preference in egg placement.

The eggs usually lined the tunnel walls (Fig. 16). They were deposited in rows or scattered throughout the margins of the tunnels of the gallery. The area of the gallery near the entrance where the male was located was usually free of eggs.

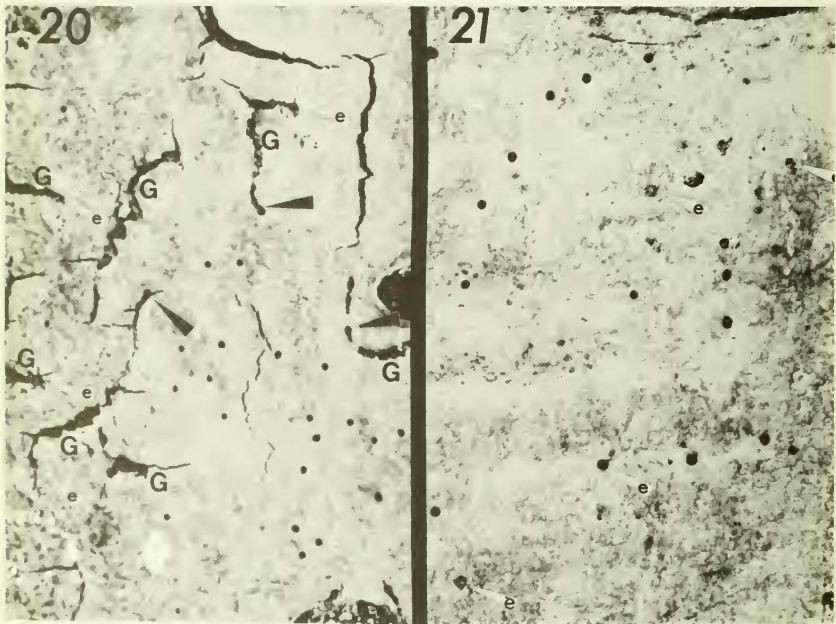
The incubation period for *P. mucronatus* was longer than for *T. populi*. The larvae were seldom collected with eggs, and one gallery contained 20 eggs with no larvae. Compared to *T. populi*, fewer eggs were laid and the female took greater care in depositing them, apparently to insure their survival. The larger size of the egg may be the reason why fewer were laid than in *T. populi*. The egg niche appeared to support, protect, and hold the egg in place. The boring dust packed around the egg (Figs. 16, 17) apparently holds it in place, insulates it, may serve for food when the egg hatches, and may protect it from predators.

LARVAE.—The superficial appearance of the larva was similar to *T. populi*. The length, distribution, and number of setae on the larval head capsule were characteristic of the species (Fig. 23). Widths of the head capsules of 91 larvae from 5 trees were

measured as follows: 31 from 4 trees were .24-.29 mm ($.27 \pm .013$ mm), and 60 from 5 trees were .33-.40 mm ($.36 \pm .021$ mm). The index obtained from the means was: $.36/.27 = 1.33$. Those .24-.29 mm were categorized as Instar I and those .33-.40 mm as Instar II. Head capsules were wider than comparable stages of *T. populi*.

The feeding patterns of the larvae indicated that more bark per given area was utilized in *P. mucronatus* (Fig. 18) than in *T. populi* (Figs. 6, 7), possibly resulting in more larvae per unit area.

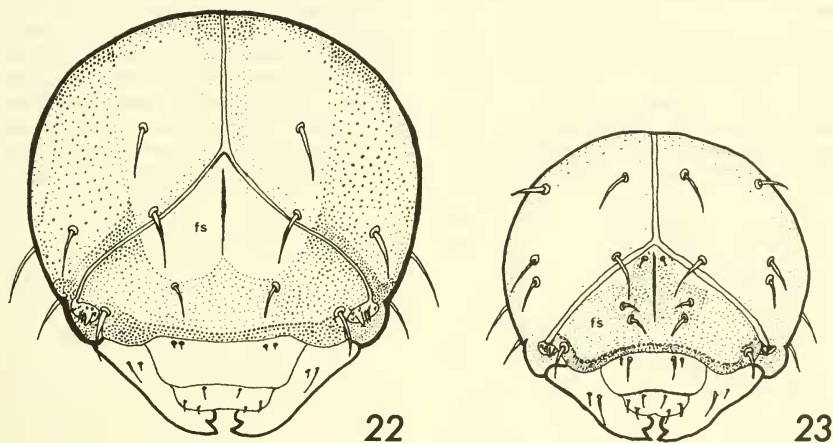
ADULTS.—The adults that emerged in the laboratory 5 February-1 March 1975 (163 and 237) and 30 March-5 April 1976 (75 and 170) all totaled gave the sex ratio (male:female) of 1:1.7 (Table 9). Lengths were determined for 100 of these emergents (35 males and 65 females). The males were 1.92-2.41 mm ($2.20 \pm .117$ mm) and the fe-



Figs. 20, 21. Bark of dead aspen after brood has emerged; primary gallery (G), gallery entrance (e, white pointer), parental adult exit hole (black pointer), and exit holes of brood adults (unlabeled holes): 20, *Trypophloeus populi*, bark split above primary galleries; 21, *Proctryphalus mucronatus*, bark not split above primary galleries and entrances plugged with frass.

males were 1.96-2.53 mm ($2.29 \pm .109$ mm). These measurements were taken from emergents of 30 April, 2 May, and 3 May. The length means for the emergents of each of these days were 2.32, 2.29, and 2.26 mm for the females and 2.27, 2.18, and 2.21 mm for the males. The emergents of the first day were longer than the subsequent ones.

OVERWINTERING.—All life stages overwintered except the eggs and pupae (Tables 8, 10). There was mortality in the parental adults that overwintered in the new primary chambers, but some also survived. The empty gut appearance of larvae collected November 1975 and March and April 1976 (Table 10) indicated that the larvae were



Figs. 22, 23. Larval head capsules: fs, frontal shield: 22, *Trypophloeus populi* (Instar III); 23, *Procryphalus mucronatus* (Instar II).

Table 9. Number of reared males and females in the first hundred to emerge per week (5 February 1975 to 1 March 1975) and per day (30 April 1976 to 5 May 1976). (*Procryphalus mucronatus*).

Collection date	Emergence dates	(n)	(n)
29 Jan 1975	5-8 Feb	45	55
	8-19 Feb	27	73
	19-26 Feb	37	63
	26 Feb		
	1 Mar	54	46
	Totals	163	237
23 Apr 1976*	30 Apr	7	42
	1 May	13	36
	2 May	16	27
	3 May	17	23
	4 May	12	23
	5 May	10	19
	Totals	75	170

*Life stages present: adults and Instars I and II.

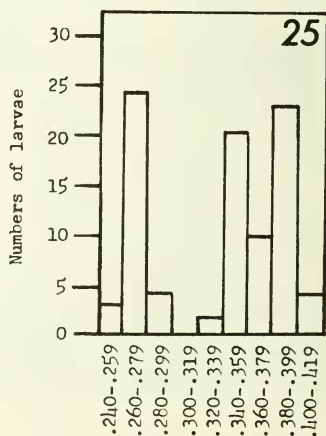
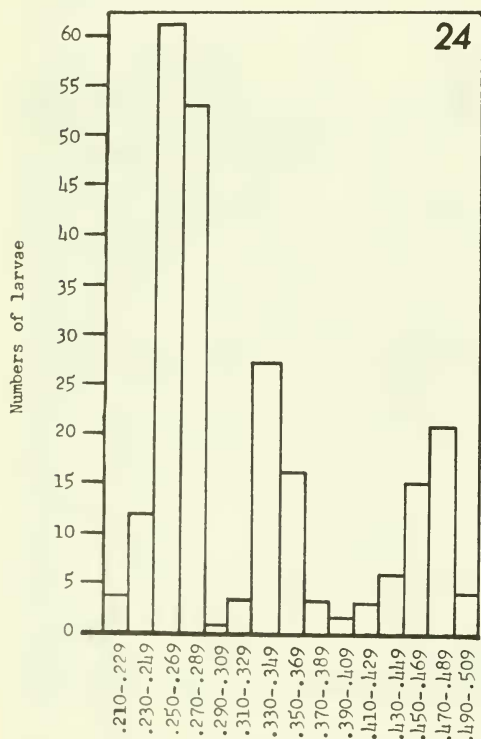
dormant during the winter. Overwintering larvae were found as deep as 7 mm from the surface of the bark. Because parental and newly transformed adults were found successfully overwintering, the adults may have some mechanism that enabled them to survive the cold winter months, a mechanism which was not present in *T. populi*.

The first eggs of the new season were laid from one to two months earlier than in *T. populi*. The overwintered adults were ready to start new galleries and lay eggs as soon as the weather warmed up.

SEASONAL OCCURRENCE.—The eggs of the first generation were found as early as 24 May. One tree was under initial attack 17 June 1972. By August 1972 (58 days later),

pupae and newly transformed adults were present. In the laboratory rearing, the duration of time from the initial attack to the next generation was 60 days in one gallery.

The seasonal occurrence of the various life stages (Table 8), the abundance and presence of overwintering stages (Table 10), and the two-month life cycle in one tree in the field and in one bolt in the laboratory indicated that there were one and one-half to two generations per year and that the overwintered adults laid the first eggs of the next season. These were followed by the eggs laid by the adults that developed from the overwintered Instar II larvae. Adults that developed from the overwintered Instar I larvae may have a later egg-laying period.



Figs. 24, 25. Numbers of larvae per size class of head capsule widths: 24, *Trypophloeus populi*, 232 larvae measured from 8 trees; 25, *Proctryphalus mucronatus*, 91 larvae measured from 5 trees.

TERRITORIAL BEHAVIOR.—The intraspecific territorial behavior consisted of the attempts of one beetle to take over another's place at the entrance to the primary gallery. Conflict for territory occurred between males and between females: between two females when one female tried to replace another female who had started her primary gallery, and between two males when one male tried to replace another male who had joined a female. The intruding beetle removed the resident by butting him (her) until he (she) backed out or was pushed out of his (her) entrance. This territorial behavior did not take place when the resident beetle was below the surface of the bark. At least half of the body of the resident needed to be protruding above the surface of the bark for an intruder to be successful.

Combat between females was observed as follows: (1) The intruding female butted the defending female until she backed out of her gallery. (2) Both beetles repeatedly met head on (prothorax to prothorax). In this position they butted each other back and forth (Fig. 26, a). (3) The beetle with the apparent advantage repeatedly extended her front legs (Fig. 26, b) in an effort to dislodge the other from the tree (Fig. 26, c). The asperities and marginal teeth on the prothorax appeared to be well adapted for butting and dislodging. Dislodgment of one of the beetles from the tree also resulted from butting without extension of the legs. Butting occurred head on, from the side, and

from behind. Very often the less aggressive of the two contenders was driven away before dislodgment occurred. When an intruder located a defender who was too far into the gallery to be butted out, he either moved on or, apparently, tried to pull the defender out by claspings onto the posterior end of his elytra with his mandibles.

In both beetle species, the territorial behavior display was by the adult males, and females apparently selected for the more vigorous males at the new gallery.

MATING BEHAVIOR.—When a male located a female who was starting a gallery (Fig. 11), he either moved on or copulated with her (Fig. 12) and then continued to search for other females. For example, three males copulated in a 25-minute period with one female who was starting the primary gallery. The duration of each copulation was 5, 3, and 3 minutes. Copulations of one other female with three males lasted for 3, 8, and 10 minutes. Repeated copulations were commonly observed. On three occasions a male was observed copulating with a female that had not yet located a site to initiate the gallery (Fig. 10). This promiscuity apparently insured fertilization even though the females outnumbered the males nearly two to one. Lone females were frequently found in plugged galleries with eggs and larvae, but no parental male.

When a male located a female that was below the surface of the bark, he performed a mating behavioral sequence. The sequence

TABLE 10. Relative abundance of overwintering life stages of *Procryphalus mucronatus*.

Collection date	No. of trees sampled	Eggs	No. of immatures			No. of adults		Feeding larvae (%) ^c
			Instars		Pupae	Trans-formed ^a	Parental ^b	
			I	II				
11 Nov 75	3	0	27	63	0	86 ^d	1 ^e	<10(?)
9 Mar 76	1	0	4	76	0	20	0	0
23 Apr 76	1	0	20	24	0	0	0	84
23 Apr 76	4	0	p ^f	p ^f	0	0	p ^f	(?)

aln pupal cell or brood gallery

^aIn primary gallery.

^bPercent of larvae that appeared dark because of bark in their intestines. All the rest were white—their gut devoid of food material.

^cThere were 60 females and 26 males.

^dFemale.

^ePresent, but numbers were not determined.

consisted of three distinct antics: nudging, stroking, and positioning.

Nudging: The male repeatedly nudged the female by brushing across the posterior end of her abdomen with his mandibles (Fig. 27). This motion was repeated from 6 to 12 times at a rate of approximately 4 per second (sample size: $n = 18$).

Stroking: The male vigorously (approximately 7 strokes per second, sample size: $n = 1$) stroked the female's abdomen with his prothoracic legs. It appeared as though he stroked both legs at the same time. He was positioned at the edge of the entrance (Fig. 27).

Positioning: The male put his mandibles

TABLE 11. Comparison of characteristics of *Trypophloeus populii* and *Procryphalus mucronatus*.

Category	<i>T. populii</i>	<i>P. mucronatus</i>
Attack	<ol style="list-style-type: none"> 1. Live bark that is green—unhealthy trees 2. Mass attack—entire tree 3. Kills unhealthy trees 	<ol style="list-style-type: none"> 1. Dying bark that is orange or brown, fermenting, and soft 2. Scattered or mass attack—bole of the tree 3. Little effect on decline of host
Primary gallery	<ol style="list-style-type: none"> 1. Cave-type plus food tunnel and secondary egg chamber 2. Parents often exit 3. Male blocks entrance 4. Bark covering gallery usually splits 	<ol style="list-style-type: none"> 1. Linear, tunnel-type 2. Parents seldom exit 3. Entrance often plugged with frass; male inside gallery 4. Bark seldom splits
Eggs	<ol style="list-style-type: none"> 1. Egg cluster 	<ol style="list-style-type: none"> 1. Egg niches
Larvae	<ol style="list-style-type: none"> 1. Three instars 2. Four prominent setae on frontal shield; 10 other prominent head capsule setae 	<ol style="list-style-type: none"> 1. Two instars 2. Six prominent setae on frontal shield; 14 other prominent head capsule setae
Larval mines	<ol style="list-style-type: none"> 1. Distinct larval mines; fully plugged with frass 	<ol style="list-style-type: none"> 1. Larvae enlarge primary gallery; mines short, partially plugged with frass
Overwintering life stages	<ol style="list-style-type: none"> 1. Larvae only 	<ol style="list-style-type: none"> 1. Larvae and adults
Generations per year	<ol style="list-style-type: none"> 1. 1-1½ 	<ol style="list-style-type: none"> 1. 1½-2
Territorial behavior	<ol style="list-style-type: none"> 1. Butting 	<ol style="list-style-type: none"> 1. Butting and extension of prothoracic legs
Male mating behavior	<ol style="list-style-type: none"> 1. Position directly over entrance 2. Nondescript stroking, all legs in motion 	<ol style="list-style-type: none"> 1. Position at edge of entrance 2. Nudging, stroking (prolegs only), positioning jerks
Antennal position when walking	<ol style="list-style-type: none"> 1. Extended forward at 45-degree angle from side of head 	<ol style="list-style-type: none"> 1. Extended at right angle to side of head

in contact with the abdomen of the female. He apparently clasped the posterior margin of her elytra with his mandibles and also grasped her with his prothoracic legs. In this position, he often jerked the posterior end of his body up and down. He jerked from 5 to 11 times at a rate of approximately 2 per second (sample size: $n=11$). It appeared as though he was trying to position her or stimulate her to position herself for copulation. She appeared to be very uncooperative. She repeatedly backed part way out of the entrance to remove boring dust and then went back in to continue excavation.

The sequence of nudging, stroking, and positioning took approximately 2, 3, and 10 seconds, respectively (sample sizes: $n=18$, 18, and 8). The jerking antic (which was part of the positioning antic) took approximately two seconds (sample size: $n=11$). The entire sequence was usually repeated several times before copulation was successful. From 3 to 30 minutes elapsed from the time the male located the female until copulation.

The apparent reasons for the mating antics were to insure intraspecific mating and

prevent wasted time and energy in attempts to mate interspecifically. It was not unusual to find both *T. populi* and *P. mucronatus* attacking the same tree. The antics of *P. mucronatus* were more complex and apparently more advanced phylogenetically than in *T. populi*.

LOCATING INFESTED TREES.—Infestations of *P. mucronatus* were found in the same aspen groves as *T. populi* infestations and sometimes in the same tree. Diseased trees with fermenting bark were commonly attacked. Unhealthy trees typically died faster on the side that received the greater exposure to the sun. Sometimes *P. mucronatus* attacked this side while *T. populi* attacked the healthier, shaded side. Sometimes both species were in the same part of the tree, but *P. mucronatus* attacked several weeks after *T. populi*. Trees from which brood had emerged (*P. mucronatus*) did not have split bark covering the galleries, and many of the gallery entrances were still plugged with frass (Fig. 21).

HOST DAMAGE.—Infested trees were usually diseased and infested with cerambycids and buprestids. The symptoms of the fungi *Cenangium singular* (Rehm.) Davidsen and

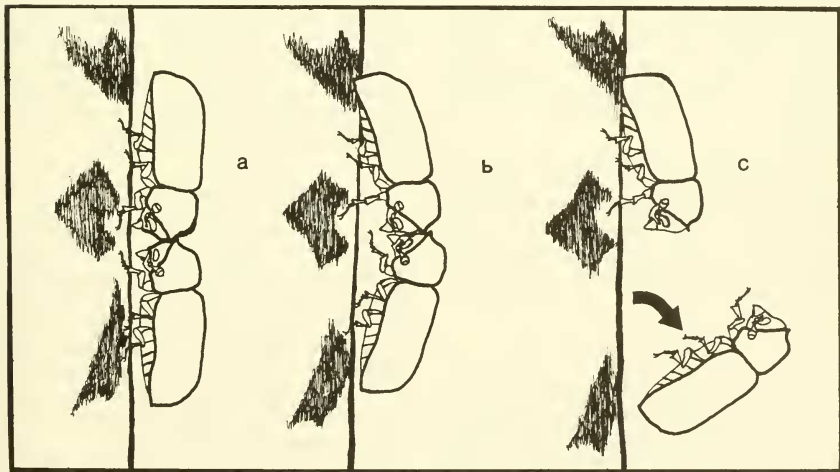
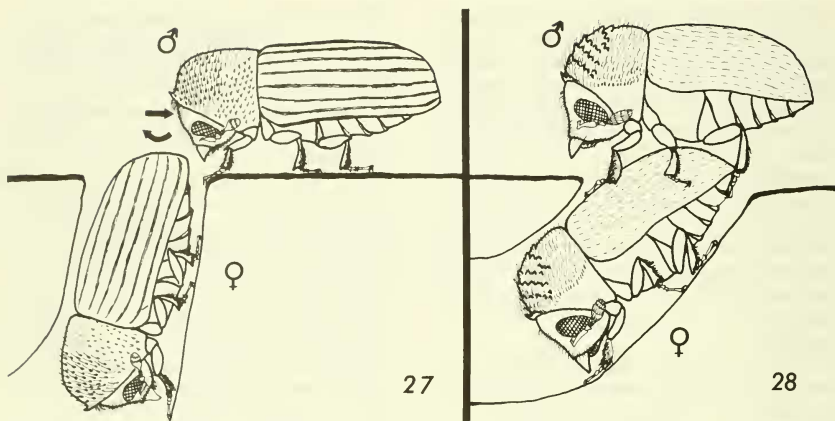


Fig. 26. *Procryphalus mucronatus*, territorial dislodgement behavior: a, butting; b, extension of prothoracic legs; c, dislodgement.



Figs. 27, 28. Mating ritual positions: 27, *Proccryphalus mucronatus*; 28, *Trypophloeus populi*.

Cash, and *Cytospora* spp. appeared on many of the infested trees. The following beetles were reared from *P. mucronatus*-infested bolts: *Trypodendron retusum* (LeConte) (Scolytidae); *Saperda calcarata* Say, *Parallelina filicornis* Casey, and *Xylotrechus annosus* Say (Cerambycidae); and *Agrilus anxius* Gory and *Dicerca tenebrica* (Kirby) (Buprestidae).

Two trees were studied that were half dead. The bark of the dead half was heavily infested with *P. mucronatus*; nevertheless, the leaves that were present remained healthy and green from June to the end of the season.

These beetles (*P. mucronatus*) were seldom important in hastening the death of the host. They accelerated the decomposition process of dead parts of the tree. They tunneled and mined in the outer bark while the other borers attacked the cambium and xylem of the host.

SUMMARY

There are behavioral aspects and morphological characters that clearly distinguish *T. populi* from *P. mucronatus* in all stages with the exception of the pupae, which were not studied in detail in this work (Table 11). Both species play an important

role in the decomposition process of diseased and weakened aspen. Probably the most unusual discovery of this research was the territorial and mating behavior. An unexpected outcome was the success in locating *T. populi* in sufficient numbers to include it in the study. These beetles were associated with many other arthropods. Over 30 species of mites were collected from the beetles and their galleries. Most were phoretic; some were predacious. In addition, over 50 species of parasites and predators were collected and reared from the aspen infested with these beetles. A list of these species is in preparation.

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